Non-goal directed recall of specific events in apes after long delays

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Abstract

We examined if apes spontaneously remember one-time, distinctive events across long delays when probed by discriminant cues. Apes witnessed an experimenter hide a cache of food, which they could then retrieve. Apes received one of two food types; one more distinctive than the other. Two, ten or fifty weeks later the apes returned to the same enclosure and found a piece of the previously hidden food on the ground. An experimenter who had not hidden the food was present. Apes immediately searched the location where the food was previously hidden (no food was here), showing recall of the event. One week later, apes returned to the same enclosure, with the same food on the ground, but now the experimenter that had hidden the food was present. Again, apes immediately searched the hiding location. Apes that had not witnessed the hiding event did not search. There was no significant effect of food type. Retention declined from exposure to the two-week delay, then leveled, consistent with the forgetting curve in humans [1]. This is the first study to show apes can recall a one-time, non-goal-directed event longer than two weeks ago, and that their recall declines in accordance with standard retention function.

Key words: great apes, spontaneous memory, episodic memory, cued recall, distinctiveness, forgetting curve.

Introduction

Ebbinghaus [1, 2] was the first to divide memory into three distinct types; voluntary, involuntary and unconscious. Involuntary memory refers to the spontaneous recollection of personal past events, often triggered by cues in the present environment (cued recall) [3]. One of the most famous examples of an involuntary memory comes from the French author Marcel Proust [4], who described the taste of a Madeleine cookie dipped in lime tea eliciting his childhood memory of visiting his aunt on Sunday mornings. Involuntary memories are a frequent occurrence in our day-to-day lives [3, 5, 6].They are often triggered by features of the present situation that match parts of the remembered event [7, 8]. Unlike voluntary memories, they are not goal-directed and strategically retrieved, rather they reflect a bottom up, stimulus-driven associative process, resulting in significantly faster retrieval times for involuntary over voluntary memories [9, 10].

Numerous studies have shown that animals can recall past events [11-19]. However, only recently has it been proposed that animals may also recall past events spontaneously, that is, involuntarily [7, 20-22]. Because involuntary memories occur spontaneously, with little effort, and are non-goal-directed, they do not rely on executive control processes or recruit pre-frontal brain regions as much as voluntary memories [23, 24]. Consequently, they are considered to be the more basic mode of remembering that proceeds the evolutionary development of voluntary memory [7, 20]. As such, if animals are capable of recalling past events strategically (voluntarily), then it follows that they should also be able to recall events via the more basic, and evolutionary earlier, involuntary counterpart.

There is some evidence that animals can recall past events spontaneously, when presented with relevant contextual cues [14, 16, 19, 25-28]. For instance, Martin-Ordas, Berntsen and Call [25] tested great apes on their ability to remember two similar tool hiding

events. In the first study, apes were presented with a task that required a tool to obtain food. After a 15-minute delay, the apes witnessed an experimenter hide two tools in two different locations, only one was useful to solve the task. The apes experienced this four times. Three years later, they were presented with the same task in the same room, and the same experimenter, however, this time the tools were already hidden in the same locations as before. Apes spontaneously searched the previous locations, and upon finding the appropriate tool, successfully completed the task. A second experiment followed the same procedure, except the apes received a slightly different task and tool, and were only presented with it once. After a 2-week retention period, apes immediately and spontaneously searched the location where the tool was hidden two weeks previously.

These studies show that apes can remember and distinguish between events in their past when features present at the time of encoding are also present at retrieval, and furthermore, that they remember almost instantaneously. This fast cued recall is consistent with the way in which involuntary memories are recalled in humans [3, 9]. However, as the apes needed a tool to complete the task, it is possible that retrieval was goal-directed, that is, they strategically and voluntarily recalled the memory. Many of the studies that show cued recall of a past event in animals incorporate goal-directed tasks [14, 19, 26, 27], and as such direct evidence for involuntary recall of events in animals is limited.

However, a study by Kano and Hirata [16] showed apes ability to recall a past event using a non-goal-directed task. Apes viewed a short movie of a novel event in which an aggressive 'King Kong' character entered through one of two doors. An eye-tracker monitored the ape's gaze during this viewing. Twenty-four hours later, while the apes watched the same video again, they made anticipatory looks at the door in which the 'King Kong' character had entered the day before. Thus, apes recalled the event 24 hours later when cued with the preceding parts of the movie. Critically, the apes were given juice or fruit to eat

during viewing of the movie, regardless of their gaze behavior, thus their recall of the event was not goal-directed. As such, this paradigm is much more in keeping with the way in which involuntary memories are retrieved, that is, via non-goal-directed cued recall, and provides evidence of the occurrence of involuntary memories in animals.

Although such studies may provide evidence for involuntary recall of events in animals, a number of questions are left unresolved. First, although it has been shown that apes can recall past events that took place as long as three years ago [25], this long retention was shown using repeated exposures during learning, meaning that the to-be-remembered event was a repeated (non-specific) event. Involuntary memories are more often of single occurring events rather than repeated ones [9, 29-31]. Furthermore, repeated events may be intentionally encoded and recalled as semantic, rule-based knowledge, due to the expectation that they will occur again [see 32]. That is, if one expects to be asked where a tool was last seen, one may simply learn through repeated associations where the tool item is located, rather than recalling the memory of the hiding event. As such, to specifically test for involuntary recall of an event in animals, the test needs to focus on recall for single exposures. In apes, such recall has only been shown for retention intervals of up to two weeks [25].

Second, despite previous studies using distinctive events [16, 25, 28] it has yet to be specifically addressed whether a distinctive event is more likely to be recalled than a less distinctive event. It is known that involuntary memories are often about distinctive events [3, 10], and that distinctiveness can improve performance in various memory tasks in rats [33-35] and primates [36, 37], but it is unknown whether it improves long-term recall of a one-time event in non-human animals.

Lastly, it is unclear whether different types of cues are equally successful at cueing recall of a past event. For instance, a study by Mendes and Call [28] incorporated social and non-social cues in a foraging event. They found apes could successfully recall the foraging locations, but acknowledged that they did not disentangle whether the memory for the locations was cued by the social, non-social, or a combination of cues. Similarly, Martin-Ordas, Berntsen and Call [25] incorporated the identity of the experimenter as a social cue, but did not test whether it was this cue or other contextual cues (room, apparatus) or combinations thereof that triggered recall of the event. There is some evidence that apes can recall information about the identity of a person from a past event [38], however, this was found using a forced recognition paradigm after a fairly short (24 hour) delay.

We investigated these aspects within one paradigm. We tested whether three species of great ape could recall a distinctive, one-time hiding event after a minimum of a 2-week retention period. During the hiding event, all food was retrieved by the subject, ensuring that there was no expectation or goal of returning to the room to retrieve the food. Furthermore, at retrieval, no task was presented to the apes in which the goal was to obtain food. As such, any recall of the hiding event was likely to be spontaneous rather than a voluntary, goal-directed response. Additionally, we manipulated three variables. First, we included three delay periods; two weeks, ten weeks, and fifty weeks. This enabled us to look at recall over longer time periods, and to assess whether forgetting occurred over time. We used a log-scale, roughly covering a one-year time period, as this scale best reflects the rate of forgetting in human long-term memory [39].

Second, we tested whether an event that was highly distinctive would be recalled more than a less distinctive (albeit, still distinctive) event. This was achieved by manipulating the type of food hidden during the hiding event. In the less distinctive condition, subjects found a large cache of bread during the hiding event. The bread was familiar to the apes, but

was not a regular part of their diet. In the highly distinctive condition, subjects found a large cache of cardamom flavored pellets. The apes had never tasted cardamom before, furthermore, the pellets resembled standard flavored pellets given to the apes daily, and thus were intended to be surprising. We chose to make the taste/odour distinctive, as opposed to the visual appearance, to see whether apes can make use of non-visual distinctive cues, as currently there is only evidence for a distinctiveness effect with visual information [36, 37]. Furthermore, odors are often highly successful as cues for retrieving memories in humans [40, 41].

Thirdly, we tested whether the addition of a social cue would improve recall relative to when that cue was absent. Specifically, we manipulated whether the presence of the same experimenter that hid food during the hiding event would improve recall performance in comparison to the presence of a different experimenter.

In short, the aim of this study was to see whether apes could recall a one-time, non-goal directed event when presented with distinctive, diagnostic cues. Previous studies have shown evidence for involuntary recall of events after long time periods, but these have involved repeated exposures or goal-directed tasks [e.g. 1]. Furthermore, the influence of distinctiveness and overlapping of cues at encoding and retrieval has not been directly tested, neither has the forgetting rate of such memories over time. As such, we aimed to address these issues.

Methods

Ethical approval

The study was ethically approved by an internal committee at the Max Planck Institute for Evolutionary Anthropology and Zoo Leipzig. Animal husbandry and research comply with

the "EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria", the "EEP Bonobo Husbandry Manual", the "WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums" and the "Guidelines for the Treatment of Animals in Behavioral Research and Teaching" of the Association for the Study of Animal Behavior (ASAB). The dataset supporting this article has been uploaded as part of the supplementary material.

Subjects

Nineteen chimpanzees (*Pan troglodytes*; age range 9–50 years), seven orangutans (*Pongo abelii*; age range 7–36 years) and seven bonobos (*Pan paniscus*; age range 8–33 years) participated in this study, resulting in a total of 33 apes. All were housed at the Wolfgang Köhler Primate Research Center at Leipzig Zoo (Leipzig, Germany) and had previously participated in cognitive studies. None of the apes were food or water deprived, and all received a healthy and balanced diet during the testing period.

Apparatus

Apes were tested inside their sleeping quarters or observation rooms (here-after testing room). Each testing room consisted of multiple enclosures, connected to each other by hydraulic doors. For this study, two adjacent enclosures were used. Additionally, each testing room contained an area only accessible to the experimenter (experimenter area). The ape always entered the testing room via one enclosure (the right), and the food was always hidden in the adjacent enclosure (the left; see ESM, Figure S1).

The hiding location varied between subjects due to constraints of the testing rooms, but was always above the eye-line of an ape from ground level and in an area not normally used for testing. For the majority of subjects, it was located on a ledge above a hydraulic

door, accessible to the experimenter only by ladder (see ESM, Figure S1), the other locations did not require a ladder.

Two types of food were hidden (exposure food); bread and cardamom flavoured pellets. The flavoured pellets were very distinctive, as the apes had never tasted cardamom before, additionally, they looked like regular pellets (eaten on a daily basis), thus when eaten were unexpected and (most likely) surprising. The bread was less distinctive, due to being used as an occasional treat, and was not surprising in taste. Still, it was by no means common to the apes. We did not choose a completely familiar food in order to keep the hiding events comparable in nature. Thus, in both cases, they would find unexpected food, but with the added element of novelty and surprise, when the flavoured pellets were hidden.

Design

We used a mixed design with exposure food (bread; N=16, flavoured pellet; N=15) and delay (2 weeks; N=10, 10 weeks; N=11, 50 weeks; N=10) between subjects, and condition (experimental, control) and retrieval session (1,2) within subjects. Exposure food referred to the type of food that was hidden during the hiding event. The alternate food type was experienced during the control condition, but was never experienced during the hiding event (see procedure).

Apes completed both an experimental and a control condition, counterbalanced between subjects. There was a minimum of six-months between conditions (range; 182-635 days. In the experimental condition, apes witnessed a hiding event in which the exposure food was hidden. After their allocated delay, they received two retrieval sessions with the exposure food, one-week apart (range; 5-9 days). The control condition differed in that no hiding event occurred before the retrieval sessions, and the alternate food was present during the retrieval sessions. This control condition was used as a baseline for comparison with the

experimental retrieval performance. As illustrated in Figure 1, two different orders were used. In one (i) participants took part in the experimental condition before the control condition, in other (ii) the order was reversed, with the control condition preceding the experimental condition.

The first retrieval session was with an experimenter that was *not* present during the hiding event, and the second retrieval was with the experimenter that hid the food during the hiding event (see Figure 1). This enabled us to see if the apes were more successful at recalling the event when social information (i.e., the experimenter identity) overlapped at encoding and retrieval forming a social cue. For the first retrieval, the experimenter was blinded to the condition and delay the subject was participating in (i.e. control or experimental, 2, 10 or 50 weeks), so to avoid any unintentional cueing. It was not possible for the experimenter in the second retrieval to be blinded in this way, as this experimenter was aware of when and who had previously seen (or not seen) a hiding event.

Procedure

During the hiding event, the ape began in one enclosure (the right) and watched the experimenter enter the other enclosure (the left) with a ladder and six food pellets or pieces of bread in her hand (exposure food). The experimenter showed the food to the subject, climbed the ladder and hid the food in the hiding location (see ESM, Figure S1 and apparatus). The subject could see that the food had been placed there, but could not see the food itself. The experimenter left the enclosure and entered the experimenter area. The connecting door between the two enclosures was then opened so that the subject could access both enclosures. Subjects were given a maximum of five minutes to find and eat the food. If the subject failed to do so in this time, the session ended and the subject did not participate any further in the study. Only the experimental condition included this hiding event.

After the allocated delay (2, 10 or 50 weeks), the subject received two retrieval sessions, one-week apart. Retrieval sessions for the experimental and control conditions followed the same procedure. In Retrieval 1, an experimenter that did *not* hide the food during the hiding event entered the left enclosure and placed a single piece of the exposure food on the ground, directly below the hiding location. The subject was not present to witness this. The experimenter then left the enclosure and stood in the experimenter area, before the subject entered the right enclosure. After a ten-second delay, in which the experimenter was facing the subject and the subject could see the experimenter, the door connecting the two enclosures was opened and the experimenter left the testing room. After two minutes had elapsed, the experimenter re-entered the testing room and stood in the experimenter area, so that the subject could again see the experimenter. The experimenter did not look at the hiding location during this time. After ten-seconds the experimenter left the testing room. After five minutes the session finished. Retrieval 2 followed the same procedure, except now the experimenter was the one who hid the food during the hiding event. No food was present in the hiding location during the retrieval to avoid searching as a result of extraneous cues, such as odour. The control condition differed from the experimental condition in two ways: subjects did not witness the hiding event and the food that was on the enclosure floor was not the exposure food in the experimental condition, but the alternate food. For example, if subjects experienced flavoured pellets as the exposure food, they found bread on the floor. Note that two different orders were used; one in which the control condition preceded the experimental condition and one with the reverse order (Figure 1)

Coding and analysis

All sessions were videotaped and later coded as to whether the subject searched or not. A search was defined as the subject climbing to the hiding location and looking/and or searching the location with hands/feet/mouth. For instances of searching, the time taken from picking up the food from the ground to reaching the hiding location was counted (here-after latency). Twenty percent of the videos were coded by a second coder. Inter-rater reliability for searching was calculated using Cohen's kappa, and Pearson's correlation assessed the inter-rater agreement for latencies. Inter-rater reliability for searching was excellent (K=1, p=<0.001) and for latencies was high (r=.88, N=9, p=<0.01).

Our main question was whether the apes could successfully recall the hiding event, as measured by searching. To test for this, we compared whether searching differed between the experimental and control condition. Furthermore, we tested whether this difference would be influenced by delay, exposure food, retrieval session and the order of condition. Since we expected the effect of these predictors to depend on condition (experimental or control), we also included the respective four, two-way interactions.

We fitted a Generalized Linear Mixed Model with a Poisson error distribution and log link function [42, 43], with condition, delay, exposure food, retrieval session and order of condition as fixed effects, species as a controlled fixed effect, and subject as a random effect (N=33 individuals; total n=123). As a test of the combined effects of condition, delay, exposure food, retrieval session, order of condition, and their interactions, we compared the full model with a null model comprising only species and the random effects using a likelihood ratio test [44, 45]. For full details of the statistical model see ESM, model description.

For every instance of searching, we calculated the average search time (in seconds) from the ape picking up the food on the floor to searching the hiding location. We also

conducted a paired samples t-test to see whether search time changed between Retrieval 1 and Retrieval 2 in the experimental condition. This enabled us to see if the subjects that had already searched in Retrieval 1 were slower in Retrieval 2, because of finding no food in the first session. Additionally, we checked for any differences in search times between the two exposure foods in the experimental condition. For subjects that searched in both Retrieval 1 and Retrieval 2, a mean search time was calculated. Search times were then compared between groups using an independent t-test. As the Levene's test was significant, the Welch-Satterthwaite calculation was applied. Likewise, search times between the three delay groups were compared (with mean search times calculated as above) using a one-way ANOVA. As the Levene's test was significant, we ran the analysis on log-transformed data (which resulted in Levene's test being non-significant).

Results

The full model compared to the null model was significant (likelihood ratio test: χ^2=20.404, df=9, p=0.017). More specifically, the interaction between condition and order of condition was significant (χ^2=6.239, df=1, P=0.013; Figure 2a). None of the other three interactions were significant (see ESM, Table S1; Figure 2c-d). The interaction showed that subjects searched significantly more in the experimental condition compared to the control condition when the control condition was completed first (Figure 2a) Thus, subjects who had seen the hiding event were searching significantly more than subjects that had yet to see the hiding event (who never searched). Those subjects who searched in the control condition when presented second, did so despite experiencing an additional retention period of six months from the initial hiding event and delay period, and crucially, after finding no food in previous experimental retrieval sessions. This included four apes that searched in all four retrieval sessions, one of which received the 50-week delay period, and thus by the fourth retrieval

318 session was still searching, despite the fact that one year and five months had passed since
319 this subject had witnessed the hiding events and despite finding no food the previous three
320 times.

321 The lack of any other interaction showed that searching in both conditions did not
322 differ as a result of delay, retrieval session or exposure food (see Figure 2b-d). This finding
323 indicated that subjects recall did not significantly decline over the three test intervals, i.e.,
324 from 2 to 10 to 50 weeks after exposure, although the performance did decline from initial
325 exposure to retrieval (see below), and that neither the social cue nor the distinctive pellet
326 improved recall performance. Additionally, recall performance between Retrieval 1 and 2 in
327 the experimental condition was nearly identical, with all but three subjects consistently not
328 searching in both sessions, or consistently failing to search in both sessions, further showing
329 that the social cue did not aid performance.

330 The average (median) search time in the experimental condition was 9 seconds
331 (N=31, Median = 9, Q1=6, Q3 =35), and for the subjects that completed the control condition
332 second, the average search time was 12 seconds (N=11, Median = 12, Q1=5, Q3=26). This
333 means that subjects immediately searched the location. We found no change in search time
334 from Retrieval 1 (M=38.38, SE=18.23) to Retrieval 2 (M=21.38, SE=8.43) in the
335 experimental condition; $t(12) = 1.20$, $p = 0.25$, suggesting that even though the apes found no
336 food in the previous session they were just as quick to search the hiding location again.
337 Likewise, search times between the two exposure foods (flavoured pellet: M=49.06,
338 SE=25.83; bread: M=35.56, SE=19.41) in the experimental condition did not differ;
339 $t(14.85)=0.42$, $p=0.68$. Neither did search times between the delay groups of the experimental
340 condition; $F(2,15) = 1.96$, $p=0.18$). Thus, subjects search times in the experimental condition
341 were not influenced by retrieval session, exposure food or delay.

342 The fact that no significant decline was observed between the three delay intervals (2,
343 10, and 50 weeks) does not mean that performance showed no decline from the hiding event
344 to retrieval. Compared with the original 100% search rate at the time of exposure, a marked
345 decline was seen at the two week delay (where 58% searched), after which the decline
346 leveled. When we plotted the rate of searching as a function of days since the observation of
347 the hiding event (estimating the first delay to 5 minutes = .003 days) a standard forgetting
348 curve was observed (see Figure 3). Retention by time was best described by a logarithmic
349 function [$y = -4.853\ln(x) + 72.666$. $R^2 = 0.92463$].

350

351 **Discussion**
352
353 The purpose of this study was threefold. First, to investigate if apes could recall a one-time,
354 non-goal directed event. Second, to assess the importance of cue distinctiveness and cue
355 similarity between encoding and retrieval, on recall success. Third, to see whether recall
356 declined over time. Our results showed that apes could successfully recall a one-time, non-
357 goal-directed hiding event upon presentation of cues that matched the memory trace, and did
358 so almost immediately, consistent with involuntary recall of an event. The addition of
359 overlapping social information at encoding and retrieval did not improve recall relative to
360 when the information was absent. Likewise, the highly distinctive cue did not enhance recall
361 relative to the less distinctive cue. Retention showed a marked decline from learning to the
362 two week delay, then leveled, consistent with the classic forgetting curve observed in human
363 memory [1, 39].

364 The average search time from finding the food on the ground to reaching the hiding
365 location was less than twelve seconds. As the apes needed to climb to the hiding location, this
366 search time reflects a fast and instantaneous response, indicative of involuntary memory [9,
367 10, 46]. This fast response was consistent across the three delay periods, and retrieval

sessions, suggesting apes spontaneously recalled the event regardless of how long ago it occurred, and when it was last recalled. Thus, if they recalled it during the first retrieval, they were just as quick to recall it again in the second retrieval. Although fast response times are consistent with involuntary recall, we acknowledge that due to not having a comparison group completing the same action using voluntary recall, we cannot say for certain that the fast response is due to involuntary as opposed to voluntary recall

However, other support for the involuntary nature of the memory retrieval comes from the lack of a goal-directed task. Involuntary memories frequently spring to mind when one is not doing anything [1], often as a result of features in the environment matching the memory trace [3]. At retrieval, the apes were not presented with a task that needed be solved by recalling the memory, unlike previous work [25]. Instead, they were simply presented with relevant external cues that matched the hiding event, such as entering the same enclosure, and finding the same exposure food. The apes enter this enclosure daily for testing, and thus the absence of any obvious testing apparatus and task may have made the context particularly distinctive. This combination of external cues led to a unique overlap between the retrieval situation and the hiding event, and most likely cued the spontaneous recall of the event.

Additionally, we found that subjects who completed the experimental condition first, followed by the control condition, were more likely to search the hiding location during the control trials than those who completed the control condition first (of which none searched). That is, some subjects who witnessed the hiding event and searched in the two retrieval sessions (after two, ten or fifty weeks), subsequently searched six months later when a different type of food was on the ground. This is despite having not found food in the hiding location the previous two sessions. Due to the long durations involved and the lack of reinforcement for searching in every retrieval session, as well as providing a cue that did not

directly match the food at the hiding event, we did not expect subjects to search. The finding that apes did search, and thus overcame all these difficulties, is a remarkable testament to the robustness of their memory for distinctive events.

The willingness to continue searching despite finding no food goes strongly against any potential critique that the apes used associative learning to encode and recall the hiding location. The apes experienced no food in the hiding location more often than they experienced food (which occurred only once), thus any association with this location and food would have been weakened. This was further supported by the lack of difference in recall between retrieval sessions 1 and 2 of the experimental condition, that is, subjects that searched in Retrieval 1 continued to search in Retrieval 2, despite finding no food, indeed, only one subject who searched in Retrieval 1 of the experimental condition subsequently failed to search in Retrieval 2. What is perhaps more surprising is that the apes who recalled the event in the control condition did so even when the cues did not directly overlap. Here, the food on the ground was not the same as the food that had been hidden during the event. However, this finding is not completely at odds with involuntary memory. Although the overlapping of features at encoding and retrieval is often found to trigger involuntary memories, it is not the extent of the overlap that is important, rather it is the uniqueness of the overlap [47]. Thus, the uniqueness of the location of the food (directly below the hiding location) and the set up (or lack of set up) of the room may have been sufficient to cue recall of the event.

This finding is consistent with the finding that the addition of a social cue made no difference to recall, as evidenced by no difference between Retrieval 1 and Retrieval 2 in which the experimenter identity differed. This is further reinforced by the fact that only two subjects who did not search in Retrieval 1 went on to search in Retrieval 2. As previously discussed, the uniqueness of the cues rather than the sheer number of overlapping cues could

explain this result. In this case, the experimenter's identity was not a unique or diagnostic cue; both experimenters in this study have tested the apes on other tasks, and thus their identity may be associated with other memories of past experiences. The more memory traces a cue is associated with, the less likely that cue will trigger a specific episode, referred to as cue overload [48]. As the identity of the experimenter was not specific to the hiding event, it was not effective as a retrieval cue.

Alternately, it may be that the experimenter identity was confounded with the order of retrieval sessions. As the experimenter that hid the food was always in Retrieval 2, which occurred one week after Retrieval 1, it could be performance was enhanced by the matching identity but hindered by the additional retention period, resulting in no difference in performance overall. However, due to not finding a significant decline in recall from the two week to the fifty-week delay, this is unlikely. Another possibility is that the apes simply did not pay attention to the experimenter. The apes participate in many studies with many experimenters, and more often than not, the experimenter's identity is not important to the task. As such, the apes may have paid more attention to other aspects of the hiding event, resulting in the identity of the experimenter being overshadowed [49]. This could potentially explain why the addition of a social cue did not improve recall performance. As such, our results suggest that using experimenter identity as a social cue may be of limited effect at retrieval, especially in the presence of other more unique and diagnostic cues, something that is consistent with other work [50, Beran; personal communication].

With regards to the two exposure foods, we found no difference in memory recall. This was unexpected, as we predicted the novelty of the flavoured pellet to enhance memory recall. Although it is unclear why this was not the case, we propose two potential explanations. Firstly, the hiding event was very distinctive regardless of which food type was hidden, in that a human entering the enclosure and hiding a large cache of food in an unusual

location is a unique event to all the apes. Additionally, the bread was fairly distinctive in itself; it was not a common food type and thus finding a large cache of it was a rather rare occurrence. Consequently, the memorability of the event may not have been dependent upon which food was hidden. Secondly, cardamom was a completely novel flavour for the apes, and so it was possible that not all the apes liked it. During the hiding event, two of the apes (Frodo and Luiza) did not eat the flavoured pellets, with Frodo returning the pellets to the experimenter by pushing them through the enclosure meshing. As such, the reason why more apes did not search in this condition could be that the apes simply did not like the food, and thus were not motivated to search for it.

In conclusion, we show that apes can spontaneously recall a distinctive one-time, non-goal-directed event after delays as long as fifty weeks, with their rate of recall across time following a standard retention function. Furthermore, apes continue to recall this event after failing to find food in that location repeatedly. These results are consistent with involuntary memory in humans, and thus provide compelling evidence for the existence of involuntary memory in apes.

Competing interests

We have no competing interests.

Author's contributions

Amy Lewis carried out the testing, the data and statistical analysis, participated in the design of the study and drafted the manuscript; Josep Call contributed to testing, helped with the data analysis, conceived of the study, participated in the design of the study, and helped draft the manuscript. Dorthe Berntsen helped with the data analysis, conceived of the study,

participated in the design of the study, and helped draft the manuscript. All authors gave final approval for publication.

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Data accessibility

Raw data uploaded as online supplemental material

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Figure captions

Figure 1. Example of the procedure sequence. i) Depicts the experimental condition first, followed by the control condition. The subject is in the bread exposure food and 50-week delay group. ii) Depicts the alternative order; with the control condition first, followed by the experimental. The subject is in the bread exposure food and 50-week delay group.

Figure 2. Proportion of searches by condition as a function of; a. order of condition, b. delay, c. exposure food, and d. retrieval session. Numbers inside the bars represent number of data points (a-c = N x 2 trials d = N). Con and Exp refer to the Control and Experimental conditions, respectively.

Figure 3. Percentage of searching as a function of days since exposure to the hiding event (estimating the first delay to 5 minutes = .003 days). Solid black line shows the forgetting rate across the 2, 10 and 50 week delays. Dotted black line shows forgetting as a logarithmic function.

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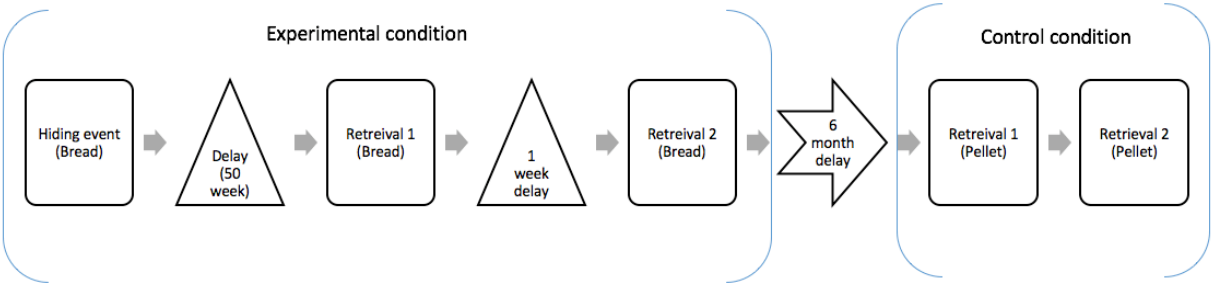

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